

DIPHASIASTRUM × *VERECUNDUM*
(LYCOPODIACEAE), *NOTHOSP. NOV.*

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ABSTRACT. Four live clones of the rare hybrid lycopod, *Diphasiastrum complanatum* × *digitatum*, have been located and studied in northern New England. This plant is described and a binomial provided.

Key Words: Lycopodiaceae, *Diphasiastrum*, hybrid

Four orthospecies and up to six hybrids of *Diphasiastrum* Holub, the flat-branched lycopods, occur in the hilly to mountainous highlands of Vermont, New Hampshire, and Maine. It is not unusual to find several species and hybrids growing together within small (< 1 ha) habitat patches. Such mixed “genus communities” (*sensu* Wagner and Wagner 1983) in northern New England present an excellent opportunity to study hybridism in the genus.

Diphasiastrum digitatum (Dill. ex A. Braun) Holub and *D. tristachyum* (Pursh) Holub are the most commonly encountered species in New England and, although locally rarer, *D. complanatum* (L.) Holub also regularly occurs, especially near and north of 45° north latitude. The fourth local orthospecies, *D. sitchense* (Rupr.) Holub, is primarily alpine in New England and consequently seldom occurs in mixed genus communities. Three hybrids are occasionally encountered in such communities: *D.* × *sabinifolium* (Willd.) Holub (= *D. sitchense* × *tristachyum*), *D.* × *habereri* (House) Holub (= *D. digitatum* × *tristachyum*), and *D.* × *zeilleri* (Rouy) Holub (= *D. complanatum* × *tristachyum*). Two other hybrids are known from only a single collection each: *D.* × *issleri* (Rouy) Holub [= *D. alpinum* (L.) Holub × *complanatum*; Wilce 1965] and *D. digitatum* × *sabinifolium* (Gilman 1994).

The sixth hybrid known from the region is *Diphasiastrum complanatum* × *digitatum*. According to Wilce (1965, p. 160), it is the “rarest of the group of hybrids involving [*D. complanatum*, *D. digitatum*, and *D. tristachyum*].” In a thorough study of herbarium specimens from Quebec, Wilce (1965) scored 95 specimens of the putative parents for morphological characters and found only three fully

intermediate hybrids, although 11 others shared some characteristics of both parents. Altogether, she was able to cite only 19 specimens of this hybrid, ranging from Quebec and Maine to Ontario, Wisconsin, and Minnesota, south to New Hampshire, Vermont, and Connecticut. However, she observed no living populations. Wagner and Beitel (1993) stated that the hybrid is “seemingly uncommon” but “probably far more common than collections indicate.” My observations indicate that in northern New England, it is rare but not significantly more so than *D. ×habereri* or *D. ×zeilleri*. I have located and studied four extant populations, each of which may consist of a single clone.

Although Wilce (1965) reported partial spore abortion in several *Diphasiastrum* hybrids, mostly well-formed, presumably viable spores were observed in the *D. complanatum* × *digitatum* hybrids reported here. Spore viability and the nearly identical morphologies of the four clones studied both suggest not just isolated individuals, but a real group of lineages able to persist over time. Therefore, recognition of the taxon as a nothospecies (a reproductively competent species of hybrid origin) is merited. Both *D. digitatum* var. *ambiguum* Vict. (Victorin 1925) and *D. complanatum* var. *gartonis* B. Boivin (Boivin 1960) were suggested by their authors to apply to plants of this hybrid origin, but have been referred to *D. ×habereri* and *D. ×zeilleri*, respectively (Wilce 1965).

Diphasiastrum* × *verecundum A. V. Gilman, *nothosp. nov.* TYPE: U.S.A. Maine: Aroostook Co., Macwahoc, large clone, uplands under powerlines, S of access road, just W of U.S. Rt. 2A, near N. Yarmouth Academy Grant town line, 31 Oct 1997, *Gilman 97395* (HOLOTYPE: NEBC; ISOTYPES: MAINE, MICH, VT). Figure 1.

Planta clavigerens, hybrida inter *Diphasiastrum complanatum* et *D. digitatum* orta; multum utrumque similata, sed pedunculo longiore, non flexile, robustiore, strobilis saepius quattuor a primo, ab altero pedunculo graciliore, ramibus secundo anno innovatis, et habitu haud flabelliforme differt.

Rhizome indeterminate, long-creeping to > 1 m, freely branching and forming large clonal patches, superficial to slightly buried, terete, 1.5–2.3 mm in diameter, loosely invested with widely spaced, short, narrow microphylls (hereafter “leaves”), these 1.8–3.0 mm long, 0.5–1.0 mm wide at base. Upright branch systems determinate, 10–16 cm tall (or with peduncles and strobili to 15–25 cm); axes terete, 1.5–2 mm in diameter, with widely spaced, short, narrow leaves, these 1.0–2.0 mm

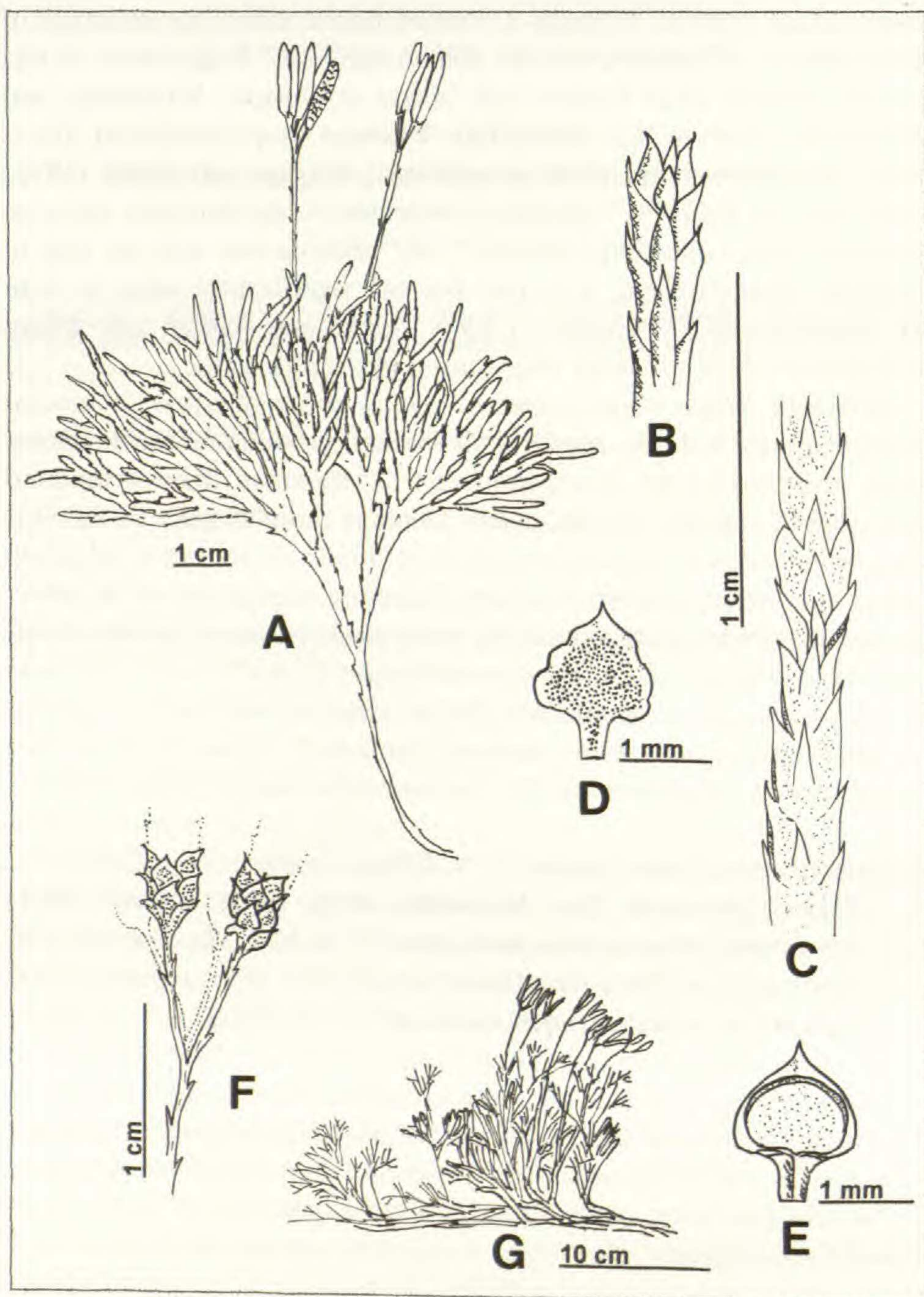


Figure 1. *Diphasiastrum xverecundum*. A. Habit of one upright branch system. B. branchlet tip, dorsal view. C. Branchlet with annual constriction, ventral view showing stomata (schematic). D. Sporophyll, abaxial. E. Sporophyll, adaxial, with sporangium at dehiscence. F. Peduncle, pedicels, and base of strobili. G. Habit of entire plant. A–F drawn from *Gilman 94349* (NEBC); G drawn from *Gilman 97395* (NEBC).

long, 0.5–1.0 mm wide at base. Lateral branches spreading, dorsiventral, complanate, 1–2 mm wide, (3–) 4–7 (–8) cm long, (1–) 2 (–3) dichotomized, with 2/2 phyllotaxy; annual growth constrictions evident. Dorsal and lateral leaves prominent, each ca. 1/3 width of branch, 2.5–3 (4) mm long. Lateral leaves adnate for 0.8 their length, leaf tips hyaline, cuspidate, normally porrect, parallel to branch orientation, appressed or (in shade forms) spreading. Ventral leaves appressed, minute, < 1.0 mm wide at base, < 2.0 mm long, narrowly triangular with hyaline tip. Stomata abundant on ventral branch surface, lacking on dorsal surface. Fertile branches similar to main axis of upright branch systems, erect, terete or (if reclining) slightly complanate, 1.5–3 mm in diameter, (5–) 10–20 (–30) mm long, closely invested with numerous short, broad leaves imbricate in apparent 1/7 or 1/8 phyllotaxy; stomata abundant on abaxial leaf surfaces. Peduncles erect, slender but not flexuous, 0.8–1.2 mm in diameter, (2–) 3–6 (–7) cm long, often twice dichotomized to form 4 pedicels, angle of dichotomy narrow, 35°–40°. Peduncle leaves scattered, narrow, somewhat hyaline, usually spreading. Pedicels often four, with scattered spreading narrow leaves, slender, 0.5–0.9 mm in diameter, altogether (from base of first dichotomy) 5–15 mm long, individually (from base of second dichotomy) 2–11 mm long. Strobili 1–4 (–5), with well-defined bases, 3 mm in diameter, (1.6–) 2.0–2.5 (–3.0) cm long. Sporophylls subpeltate, spade-shaped, tips cuspidate, spreading at maturity, central portion green, margins hyaline, erose. Sporangia reniform. Spores many hundred in each sporangium, well-formed, yellow, trilete, surfaces prominently reticulate, 35–40 μ m. Gametophyte unknown (in parents top- or carrot-shaped, subterranean, achlorophyllous, mycotrophic). Chromosome number undetermined ($n = 23$ in parents).

ETYMOLOGY. The specific epithet refers to the bashful nature of this taxon, which is rare, shows no outstanding features, and is consequently difficult to come to know.

HABITAT. Habitats are typically dry, with a shallow (1–2 cm) organic soil horizon overlying sandy or loamy soils.

Three of the four clones observed were growing in mixed-genus communities with at least four other *Diphasiastrum* taxa, including the putative parents; the fourth population was associated only with *D. digitatum*. One habitat was an old hayfield, mowed annually. The others, including the type locality, were electric transmission line corridors on lands that had previously been pastures or fields and were maintained in seral field and shrub associations at the time of this study.

Associated plant species, in addition to other *Diphasiastrum* taxa, included members of the regional upland flora typical of infertile soils, such as the mosses *Polytrichum juniperinum* Hedw., *P. piliferum* Hedw., and *Thuidium delicatulum* (Hedw.) BSG; clubmosses *Lycopodium clavatum* L., *L. hickeyi* W. H. Wagner, Beitel & Moran, and *L. lagopus* Zinserl. ex Kuzen; ferns *Pteridium aquilinum* (L.) Kuhn var. *latiusculum* (Desv.) Underw. ex Heller, *Dennstaedtia punctilobula* (Michx.) T. Moore, and *Thelypteris noveboracensis* (L.) Nieuwl.; grasses *Agrostis capillaris* L., *A. perennans* (Walter) Tuck., *Brachyelytrum erectum* (Schreb. ex Spreng.) P. Beauv. var. *glabratum* (Vasey) Koyama & Kawano, *Bromus ciliatus* L., *Danthonia spicata* (L.) F. Beauv., and *Dichanthelium boreale* (Nash) Freckmann; forbs *Anaphalis margaritacea* (L.) Benth. & Hook., *Antennaria neglecta* Greene var. *canadensis* (Greene) Cronquist, *Cornus canadensis* L., *Euthamia graminifolia* (L.) Nutt., *Hieracium pilosella* L., *Lysimachia quadrifolia* L., *Solidago nemoralis* Aiton; and low shrubs *Rubus hispidus* L., *Gaultheria procumbens* L., *Vaccinium angustifolium* Aiton, and *Spiraea alba* Duroi var. *latifolia* (Aiton) Dippel.

Diphasiastrum \times *verecundum* is much like *D. complanatum* and *D. digitatum*, but it differs from the first in a longer, less flexuous, more robust peduncle, and more often four strobili on each peduncle. From *D. digitatum* it differs in a more gracile peduncle and lateral branches growing through two or more successive years. The dorsal leaves are often slightly wider than in *D. digitatum*, although this character is difficult to assess due to variation. It also has somewhat the straggling or discomposed habit of *D. complanatum* and lacks the regular, fanlike branching habit that normally strongly characterizes *D. digitatum*.

Wilce (1965, p. 160) stated that this hybrid "is probably the least difficult to recognize and identify," based on intermediacy of characters. Unfortunately this intermediacy results in a merely "generic" appearance. There are no unique, idiosyncratic, or transgressive characters that allow immediate recognition. Field identification is aided in mixed communities by comparison with living material of the other taxa, especially if one is familiar with its progenitors as well as with *Diphasiastrum tristachyum* and its hybrid progeny. Of some aid in recognition are the small size and narrow shape of the ventral leaves (Figure 1C), features shared by its progenitors but different from the typically longer and wider ventral leaves of *D. tristachyum*. In life, *D. \times verecundum* has a bright, emerald green color, quite dissimilar from the yellow-green

color typical of *D. digitatum*, from the dull, darkish-green to yellow-green color of *D. complanatum*, and from the glaucous blue-green color of *D. tristachyum* and its hybrids. Plants from shaded habitats are particularly difficult to assess, as are dried and pressed specimens. Therefore, the above description is based on plants from the four living populations observed, all occurring in open, sunny habitats.

Relationships in *Diphasiastrum* are unresolved and the presumed hybrid origin of taxa of intermediate morphology has not been fully demonstrated. At least some hybrids are homoploids with diploid ($2n = 46$) chromosome numbers (Hersey and Britton 1981; Wagner 1980, 1992). Although Whittier and Britton (1995) succeeded in culturing gametophytes from spores of *D. \times habereri*, *Diphasiastrum* is difficult to cultivate and no hybrid has been produced in culture. Stoor et al. (1996) concluded additive isozyme banding patterns (phosphoglucoisomerase and esterase) supported a hybrid origin (*D. alpinum* \times *tristachyum*) for the European plant they named *D. oellgaardii*, but such patterns are not logically unequivocal for homoploid taxa (Vogel and Rumsey 1999). Unlike taxa of allopolyploid origin, in which a multiplied chromosome complement convincingly argues that progenitors must have preceded derivatives, so-called “additive” banding patterns in homoploids might indicate segregating, not hybridizing, lineages. Indeed, Vogel and Rumsey (1999) questioned the validity of the hybrid hypothesis for this reason. However, it is improbable that divergent speciation would have resulted in taxa intermediate in so many morphological characters as those observed. The group indeed presents a difficult puzzle that invites further investigation by imaginative means.

ADDITIONAL SPECIMENS: U.S.A. Maine: Aroostook Co., Haynesville, large clone at S edge of powerline corridor, just W of the village of Haynesville and just upslope of U.S. Rt. 2A, 24 Aug 2000, *Gilman 2K186* (MAINE, NEBC). Vermont: Essex Co., Concord, on old pasture land under powerlines (the adjacent areas having grown up to boreal forest), near Joslin Turn, 19 Sep 1999 et seqq. *Gilman 99220* (VT, NEBC); Lamoille Co., Wolcott, one large clone, old pasture, north of Eastman Cross Road, 19 Nov 1994 et seqq., *Gilman 94349* (VT, NEBC).

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